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Deterministic Model for Simulating the Predation of *Toxorhynchites rutilus rutilus* on *Aedes aegypti*

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Deterministic Model for Simulating the Predation of *Toxorhynchites rutilus rutilus* on *Aedes aegypti*

By Dana A. Focks,[1] Jack A. Seawright,[1] and Donald W. Hall[2]

ABSTRACT

A deterministic computer model detailing the interaction of the container-breeding mosquito *Aedes aegypti* (L.) and the predatory larva of *Toxorhynchites rutilus rutilus* (Coq.) is presented. Simulation runs involving the release of *Tx. r. rutilus* adults indicate that releases resulting in one larva per container are sufficient to reduce *Ae. aegypti* adult density 75% in 20 days. The slow development rate of predator immatures enables control to be maintained for several months. Simulations of predator release and the use of adulticides indicate that it is possible to obtain zero adult densities. Finally, the model demonstrates that the most important parameter in determining the degree of control established is the distribution of predator eggs. KEYWORDS: *Aedes aegypti* (L.), computer simulations, insect control (biological), insect control (chemical), mathematical models, mosquitoes, *Toxorhynchites rutilus rutilus* (Coq.).

INTRODUCTION

Historically, mosquito control has involved source reduction and insecticides. Predicting the outcome of these measures is simple and straightforward. Currently, additional methods of mosquito control are being studied, some of which involve the interaction of two species. Difficulty in understanding the dynamics of the interaction between two species makes predicting the outcome of new methods complicated. Attempting to optimize a strategy that utilizes two different methods in conjunction, e.g., predators and insecticides, is particularly difficult. Therefore, computer-simulation models are becoming increasingly popular as a tool in the development and evaluation of new control strategies.

The purpose of this paper is to (1) present a deterministic computer model examining the interaction of *Aedes aegypti* (L.) and the predatory larva of *Toxorhynchites rutilus rutilus* (Coq.) and (2) simulate the population dynamics of *Ae. aegypti* under different control strategies involving the release of *Tx. r. rutilus* adults and the use of adulticides. Pertinent to this discussion is an explanation by Mertz (1970) of methods used in life-history analysis. The utility and rationale of simulation in developing control strategies were reported by Conway (1970), Haile and Weidhaas (1976), and Weidhaas (1974).

While many of the parameter values for *Tx. r. rutilus* are from laboratory experiments conducted under conditions obviously different from those expected in the field, there remains a very real value in the model-building exercise. Characterizing the interaction of the two species highlights areas where additional information is needed. Also, simulating with the present model gives us insight into how best to approach a large-scale release experiment where prey control is to be attempted. Finally, the preliminary model gives us a framework within which to interpret the resulting experimental field data. The model is written in FORTRAN; the program listing is given in the appendix.

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MODEL DESCRIPTION

The model described herein may be called a compartment model (Miller et al. 1973). Each stage of each species is represented by a number of storage registers within an array (an array is a group of registers). The registers represent 1-day age classifications of the various stages; a particular array represents the age distribution of a particular stage or instar. Except for the *Tx. r. rutilus* larval stage, the durations of various stages and instars are determined by the number of registers within a particular array. The model is made to cycle daily by replacing the contents of the next storage register with the contents of the previous register multiplied by the daily survival for that particular stage and species; the output of the terminal registers of one array (stage) is the input to the next array (stage). Most values of daily survival for both species are fixed during any particular simulation run (table 1); the daily survival for *Ae. aegypti* first and second instars is a density-dependent variable. The length of larval life of *Tx. r. rutilus* is also a variable, it being a function of the amount of prey available. Details of these variables are presented later in the paper.

The data used for the modeling of *Ae. aegypti* immatures were largely derived from Southwood et al. (1972) and for adults, from Sheppard et al. (1969). These life-table and ecological studies were conducted in Bangkok, Thailand, in hopes of correlating *Ae. aegypti* population dynamics with the known seasonal incidence of dengue hemorrhagic fever. Surprisingly absent from both studies was any information on fecundity and ovipositional patterns; estimates for these parameters were derived from data on *Ae. aegypti* in northern coastal Florida (unpublished data). The data for *Tx. r. rutilus* came from laboratory, outdoor-cage, and field experiments conducted by Focks and Seawright (1977).

According to Sheppard et al. (1969), the main *Ae. aegypti* breeding sites in Bangkok are the earthen or ceramic water-storage jars (about 100- to 200-liter capacity) found in association with all types of housing. These jars usually contain water throughout the year and are replenished with rainwater, tapwater, or riverwater. Southwood et al. (1972) state that the water-storage jars number about 150 per acre, and about 53% of these are positive for *Ae. aegypti* immatures at any particular time. Interestingly, both stud-

Table 1.—Parameters and their values for model computations

Symbol	Description		Value
	Aedes aegypti		
SA	Daily adult survival	pct	88
F	Fecundity	No. eggs/oviposition	93
P	Successful pupation	pct	90
SE	Daily egg survival	pct	98
S	Daily survival for 3d and 4th instars and pupae	pct	95
C	Density-dependent coefficient for calculating SI[1]		0.01
SI	Density-dependent daily survival for 1st and 2d instars	pct	0–100
AEDIST	Containers positive for *Aedes* immatures	pct	53
	Toxorhynchites rutilus rutilus		
SAT	Daily adult survival	pct	88
FT	Fecundity	No. eggs/female/d	1
SIT	Daily immature survival (larvae and pupae)	pct	99
DISTBN	Containers positive for *Toxorhynchites* larvae	pct	50–90

[1] See figure 1 for details.

ies reported remarkably stable densities and distributions of all stages from season to season. Adult densities of 1,100 per acre, or 7.3 adults per container, were reported. Table 2 presents the development times for immatures and the average numbers of, immatures per container. Southwood et al. (1972) note that 20% of the embryonated eggs hatch without the flooding stimulus described by Christophers (1960) and that approximately 50% of the remaining eggs hatch with each subsequent reflooding. Since they reported no data on the frequency of jar flooding, our computer model simulates no-rain and daily-rain situations. A final feature of the population dynamics of *Ae. aegypti* in Bangkok is the density-dependent survival during the first two larval instars. The stability of the mean number of immatures per container appears to stem from a paucity of larval food (table 2); the number of new third-instar larvae is a consequence of the available food and not the number of newly hatched first-instar larvae. An algorithm for producing the observed larval densities, which is largely independent of oviposition or frequency of hatch, is detailed in figure 1.

Table 2.—Development times, average numbers, and percentages of immature *Aedes aegypti* per water-storage jar positive for *Aedes aegypti* in Bangkok, Thailand[1]

Stage	Mean development time (days)	Mean No. individuals per jar	Percentage of immatures per jar
Eggs	4.0	...	...
Larvae:			
1st- and 2d-instar	5.2	20.0	51
3d-instar	3.2	9.5	24
4th-instar	6.5	8.0	20
Pupae	2.2	2.0	5
Total[2]	17.1	39.5	100

[1] Southwood et al. (1972).

[2] Excluding eggs.

The modeling of *Tx. r. rutilus*, with several exceptions, is similar to that for *Ae. aegypti*. Figure 2 reveals that (1) the three last immature stages are separated into three arrays, (2) eggs hatch independently of rainfall on the second day after oviposition, and (3) oviposition begins 6 days after eclosion and occurs daily thereafter. Figure 2 also shows laboratory-reared adult *Tx. r. rutilus* being released at 6 days of age.

The nature and mechanics of modeling the predation of *Tx. r. rutilus* on *Ae. aegypti* are pre-

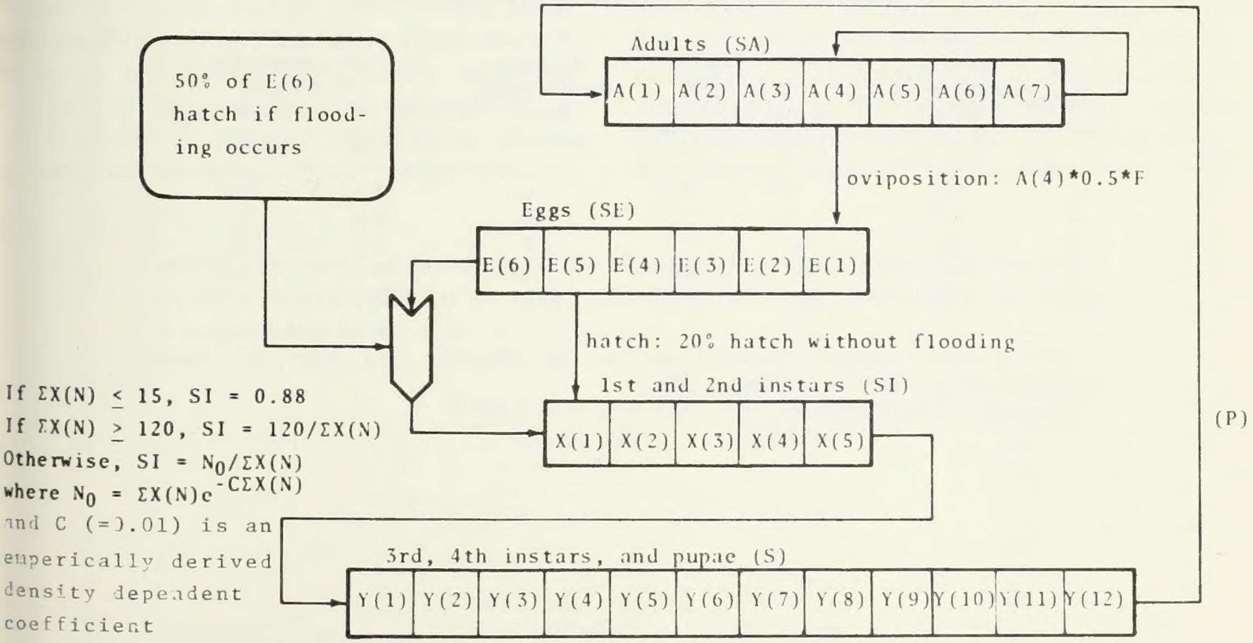

FIGURE 1.—Flow chart and algorithm for *Aedes aegypti* computations. Letters within parentheses refer to daily survival values listed in table 1.

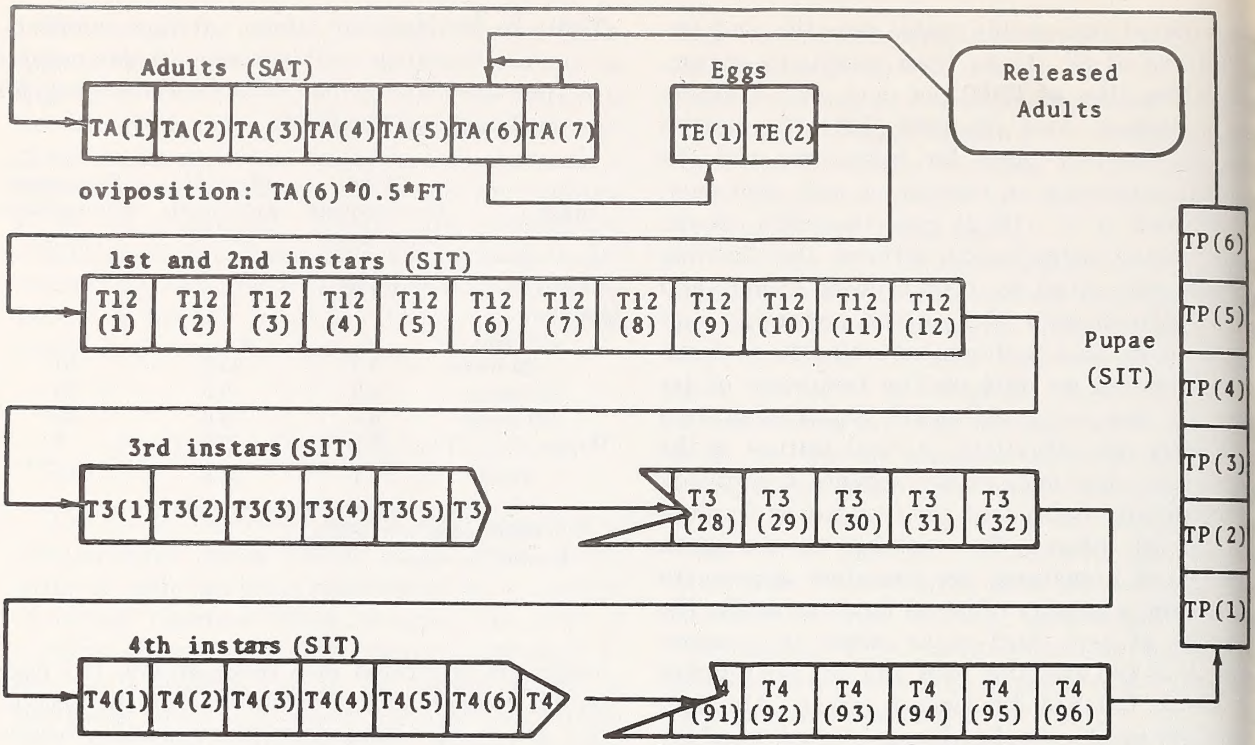
Adults (SAT)
TA(1) TA(2) TA(3) TA(4) TA(5) TA(6) TA(7)
Eggs
TE(1) TE(2)
Released Adults
oviposition: TA(6)*0.5*FT
1st and 2nd instars (SIT)
T12 (1) T12 (2) T12 (3) T12 (4) T12 (5) T12 (6) T12 (7) T12 (8) T12 (9) T12 (10) T12 (11) T12 (12)
Pupae (SIT)
TP(6) TP(5) TP(4) TP(3) TP(2) TP(1)
3rd instars (SIT)
T3(1) T3(2) T3(3) T3(4) T3(5) T3
T3 (28) T3 (29) T3 (30) T3 (31) T3 (32)
4th instars (SIT)
T4(1) T4(2) T4(3) T4(4) T4(5) T4(6) T4
T4 (91) T4 (92) T4 (93) T4 (94) T4 (95) T4 (96)

FIGURE 2.—Flow chart for *Toxorhynchites rutilus rutilus* computations. Letters within parentheses refer to daily survival values listed in table 1.

Table 3.—Larval development times of *Toxorhynchites rutilus rutilus* in the laboratory when fed *Aedes aegypti* immatures

Tx. r. rutilus instar	Average development time (days)	Average consumption of *Ae. aegypti* 1st and 2d instars		Average development time (days)	Average consumption of *Ae. aegypti* 3d and 4th instars and pupae	
		Total	Daily		Total	Daily
1	1.2	6.4	5.3	1.2	[1]6.4	[1]5.3
2	2.6	6.6	2.5	2.6	[1]6.6	[1]2.5
3	8.0	[2]60	7.5	3.8	8.0	2.1
4	32.0	[2]600	18.8	8.0	73	9.1
Total	43.8	673	. . .	15.6	94	. . .

[1] The numbers reported consumed are 1st- and 2d-instar prey, since early-instar predators cannot consume late-instar prey.

[2] Estimated from 3 replicates.

sented below. Table 3 shows the development times of and the numbers of prey devoured by various instars of *Tx. r. rutilus* when offered either early (first- and second-instar) or late (third- and fourth-instar and pupae) *Ae. aegypti* immatures. Table 4 shows how long the various *Tx. r. rutilus* instars can fast before death, and table 5 presents the duration of development for larval instars when fed *Ae. aegypti* larvae or tropical fish food.

The situation to be modeled is as follows: (1) Third and fourth instars of *Tx. r. rutilus* develop faster on a diet of late instars and pupae than on a diet of early-instar prey. (2) All larvae develop at a rate proportional to the amount of prey available until the amount of prey exceeds that given in table 3. (3) All predator instars can survive without prey for a period of time, and if provided detritus, can develop at a very slow rate up to eclosion. (4) The daily immature survival (SIT) is constant, irrespective of diet (unpublished data).

In the model, first- and second-instar predators (array T12) are assumed to eat before third- and fourth-instar predators (T3 and T4, respectively) on any particular day. This assumption simplifies the programing of predation and does not, considering the relative amounts of prey consumed by each instar, introduce significant errors. The number of storage registers within arrays T12, T3, and T4 (16, 32, and 96, respectively) do not correspond directly to 1 day each. This is because the larvae are moved incrementally within an array as a function of prey size and numbers of prey available. If no prey is available, all the predators are incremented one register forward. If the numbers of prey equal or exceed the numbers in table 3, the larvae are incremented 4, 8, and 12 registers forward in arrays T12, T3, and T4, respectively. Intermediate numbers of prey result in incrementing the predator arrays by an amount proportional to the available prey. The *Ae. aegypti* immature arrays in containers positive for *Tx. r. rutilus* (XA and YA) are updated daily for the effects of predation. Since cannibalism does not occur among the predators at the densities considered here, even when there is no prey, it is not modeled.

Table 4.—Larval life of *Toxorhynchites rutilus rutilus* in the laboratory when deprived of food

Instar in which starvation began	No. individuals observed	Age at beginning of test (days)	Days before death
1	9	0	6.9±0.3
[1]2	10	4 or 5	8.4±0.5
[1]3	10	9 or 10	18.0±6.5
[2]4	8	13	[3]59.0±22.4

[1] Temperature of 27° C.

[2] Temperature of 27° C during first 11 days, then raised to 30° C.

[3] One individual fasted 88 days.

Following a release of *Tx. r. rutilus* adults, one would expect, on the basis of the distribution of *Ae. aegypti* larvae (53% positive) and an assumed predator distribution of 80% (unpublished data), to obtain four types of containers—42.4% positive for both species, 10.6% positive for *Ae. aegypti* only, 37.6% positive for *Tx. r. rutilus* only, and 9.4% containing neither species. Since it is assumed that no *Tx. r. rutilus* adults result

Table 5.—Duration of development for instars of individually reared *Toxorhynchites rutilus rutilus* at 28°±1° C when fed diet of *Aedes aegypti* larvae or tropical fish food

Instar	Mean development time (days)[1] when fed—		Time increase, fish-food fed over prey fed (pct)
	Ae. aegypti (*n*=48)	Fish food (*n*=83)	
1	1.2	8.6	720
2	2.6	5.2	200
3	3.8	14.4	380
4	8.0	79.3	990
Total±standard deviation	15.6±1.4	107.5±19.8	690

[1] According to the arithmetic method of Southwood et al. (1972), each entry is the time required for half the population to molt to the next instar.

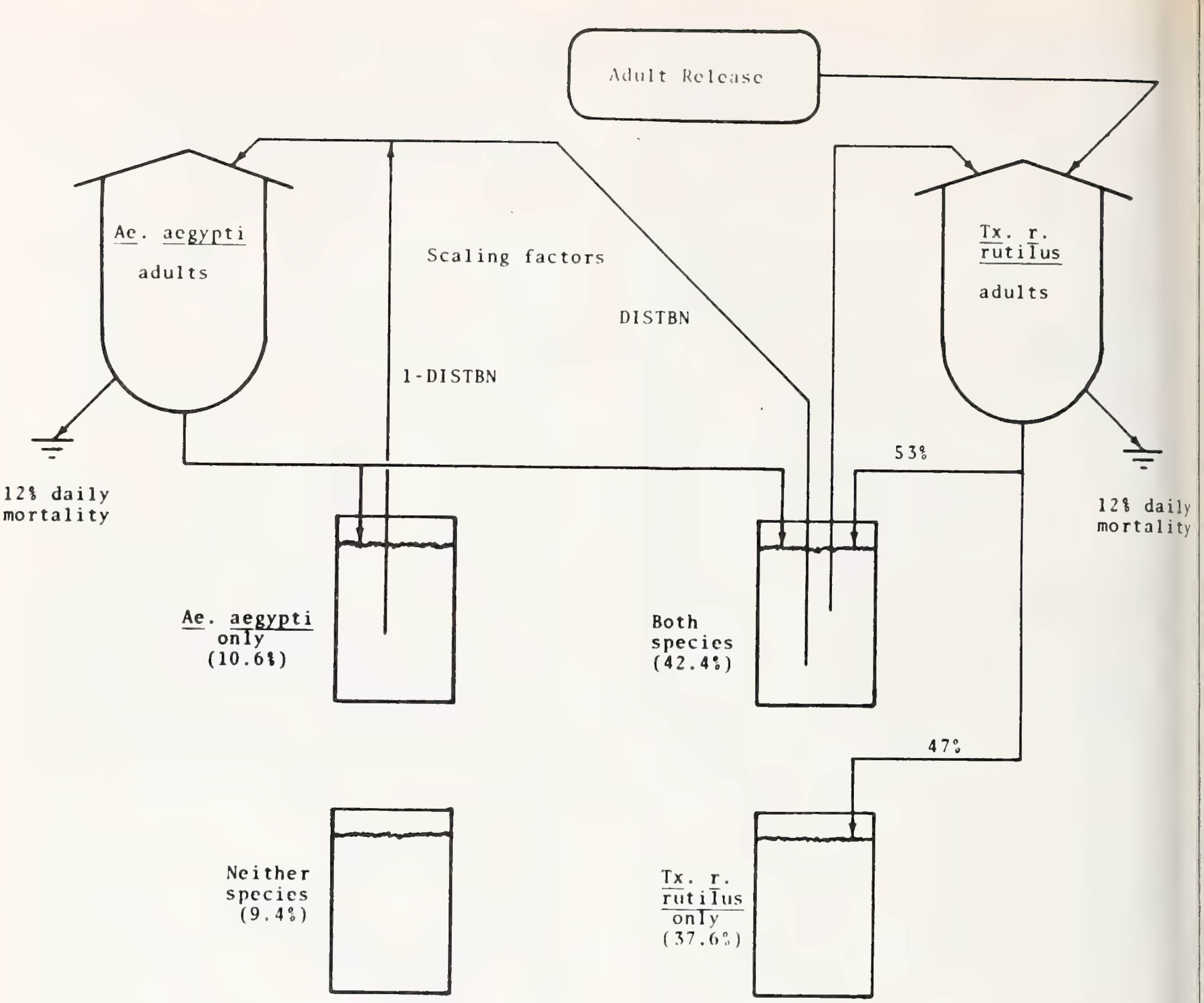

FIGURE 3.—Predator and prey distribution in containers. Percentages in parentheses refer to frequency of each type of container when 53% are positive for *Aedes aegypti* and 80% are positive for *Toxorhynchites rutilus rutilus.*

from oviposition into containers devoid of prey and since one type of container produces neither species, these containers are not specifically modeled in the program but are accounted for with scaling factors (fig. 3). To represent the salient features of the interaction in the field and to represent the resulting *Ae. aegypti* adult density, two containers, both positive for *Ae. aegypti,* are included in the model. Only one of these is interfaced with the predator subroutine. *Ae. aegypti* eclosion and *Tx. r. rutilus* oviposition are scaled by factors of DISTBN and AEDIST, respectively, to depict the frequency of the two containers in the field. Because of the scaling factors, the numbers of *Ae. aegypti* and *Tx. r. rutilus* adults are in terms of one container, and multiplying the output of adults by the number of containers per area gives an absolute population estimate.

RESULTS OF SIMULATION

Figures 4 and 5 represent model-generated *Ae. aegypti* adult densities per container for no-rain and daily-rain-into-every-container situations, respectively. Figures 6 and 7 depict the corresponding total number of *Ae. aegypti* immatures per container for the two rainfall situations. In each instance and in all subsequent simulation runs, the model program was initialized on day 1 with 7.4 1-day-old adult *Ae. aegypti.* The resulting numbers within each stage were largely inde-

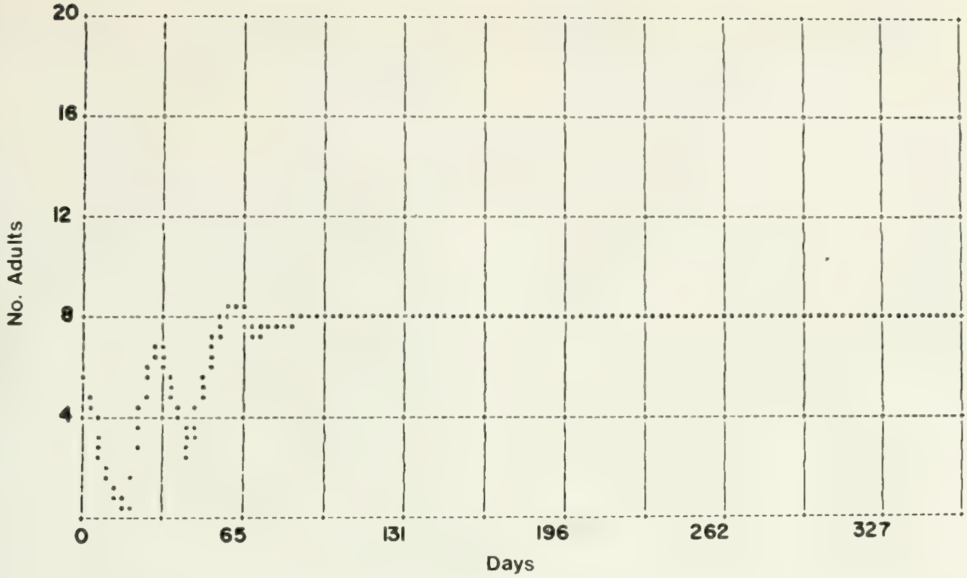

FIGURE 4.—*Aedes aegypti* adult density per container with no control measures applied (no rain).

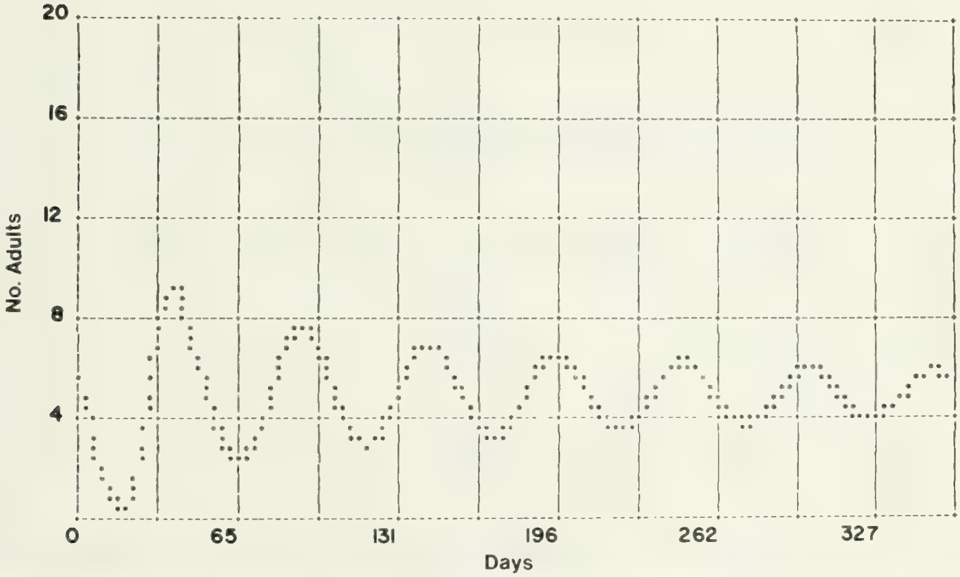

FIGURE 5.—*Aedes aegypti* adult density per container with no control measures applied (daily rainfall into every container).

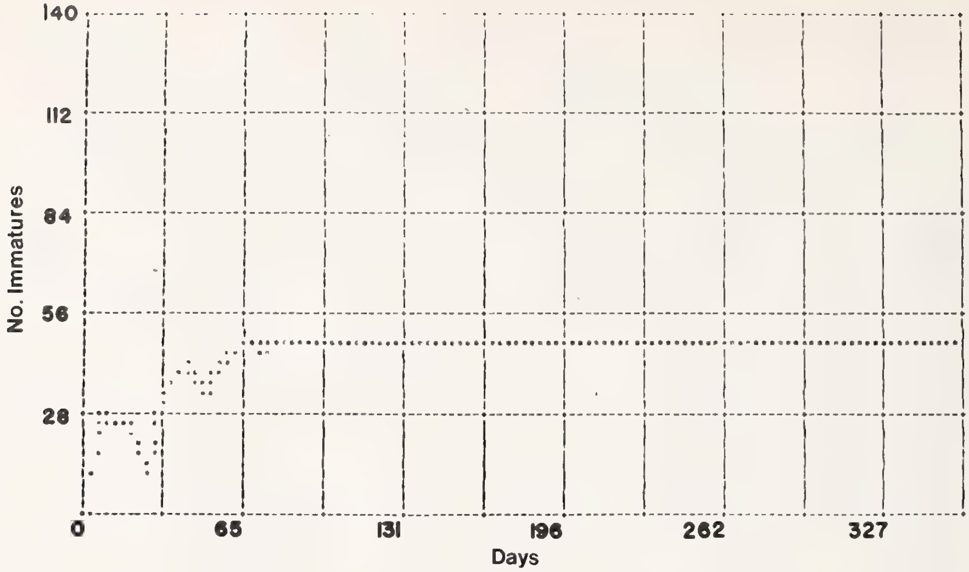

FIGURE 6.—*Aedes aegypti* immature density per container (no rain).

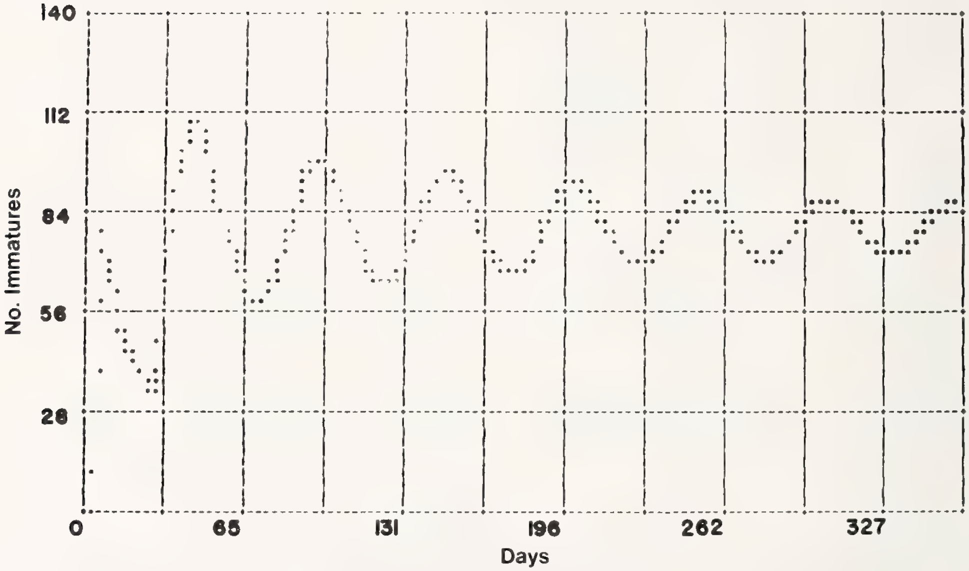

FIGURE 7.—*Aedes aegypti* immature density per container (daily rainfall into every container).

pendent of the number and stages used in initializing the model. The graphs were smoothed by plotting 4-day moving averages. The cyclic nature of the daily-rain situation in figures 5 and 7 dampened with time.

A comparison can be made from table 6 between the number of *Ae. aegypti* individuals per stage per container observed by Southwood et al. (1972) and the number of individuals per stage per container generated by the model when no control measures were applied. The total number of immatures per container generated by the model exceeded the total reported by Southwood et al. This disparity was allowed to remain because the difference was not large, especially in

Table 6.—Number of *Aedes aegypti* per stage per container as reported by Southwood et al. (1972) and the number generated by the model

Stage	Southwood et al.	Model		
		No rain	Rain[1]	Average
Larvae:				
1st- and 2d-instar	20.0	30.0	70.0	50.0
3d-instar	9.5	8.0	5.0	6.5
4th-instar	8.0	8.0	5.0	6.5
Pupae	2.0	2.2	1.5	1.9
Total	39.5	48.2	81.5	64.9
Adults	7.3	8.0	5.0	6.5

[1] Situation modeled is that all containers receive daily rain.

Table 7.—Mean number of *Aedes aegypti* per container after contact adulticide application and after application when adult density exceeded seven or four adults per container[1]

Stage	No treatment[2]	Single application[2]	7 Adults per container[3]	4 Adults per container[4]
Adult	8	8	3	2
Immature	49	49	28	21

[1] See figures 8–13.
[2] Daily immature survival (SI) of 75%.
[3] Daily immature survival of 84%. 15 applications in 262 days.
[4] Daily immature survival of 88%. 21 applications during period 98–360 days.

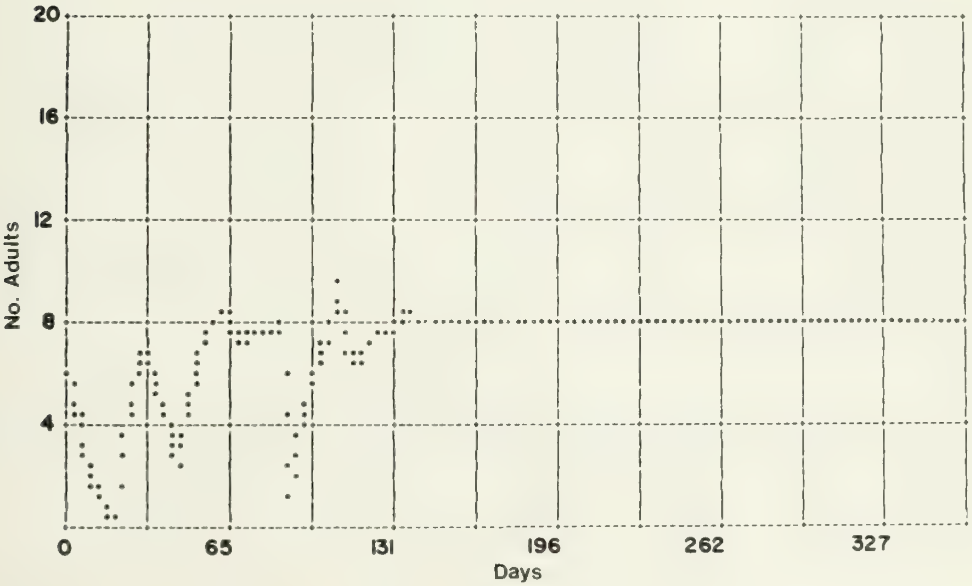

FIGURE 8.—*Aedes aegypti* adult density following contact adulticide application on day 90 (no rain). The result was 95% adult mortality with no residual effects.

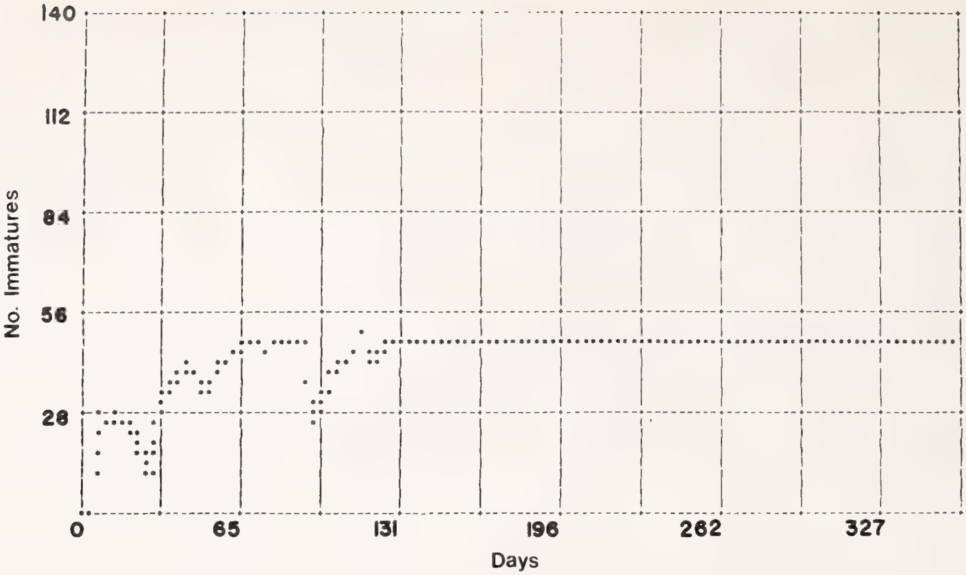

FIGURE 9.—*Aedes aegypti* immature density following contact adulticide application on day 90 (no rain).

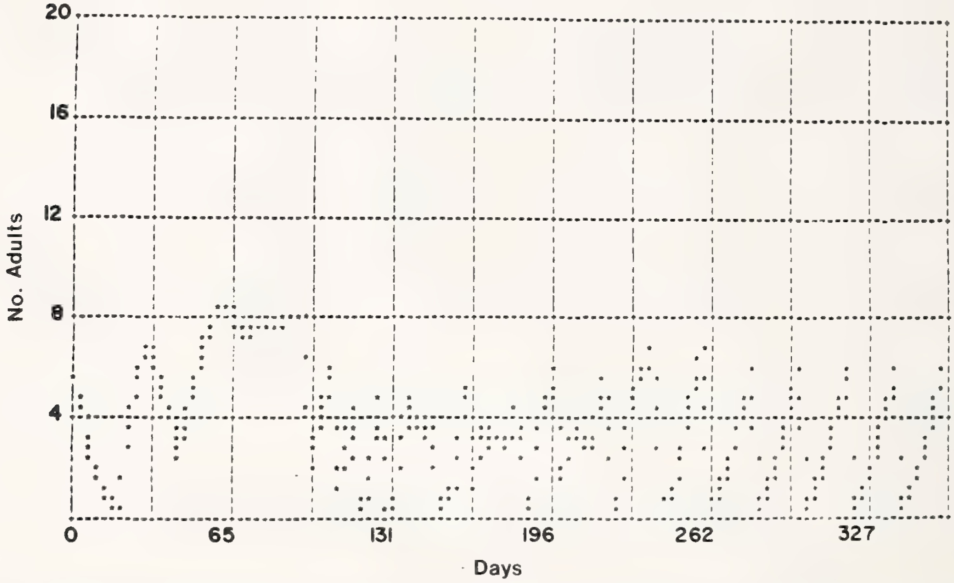

FIGURE 10.—*Aedes aegypti* adult density following contact adulticide application when *Aedes aegypti* adult density exceeded seven adults per container (no rain). Spraying at this density required 15 applications in 262 days (no rain).

the no-rain situation, and would have made the model more conservative in subsequent control simulations. Density-dependent first- and second-instar daily survival (SI) for the no-rain and daily-rain situations averaged about 75% and 50%, respectively.

The effects on *Ae. aegypti* population dynamics of contact adulticide application, which caused 95% mortality among the adults with no residual action, are presented in table 7 and figures 8–13. Figure 8 shows the overshoot of adults one generation later as a consequence of one

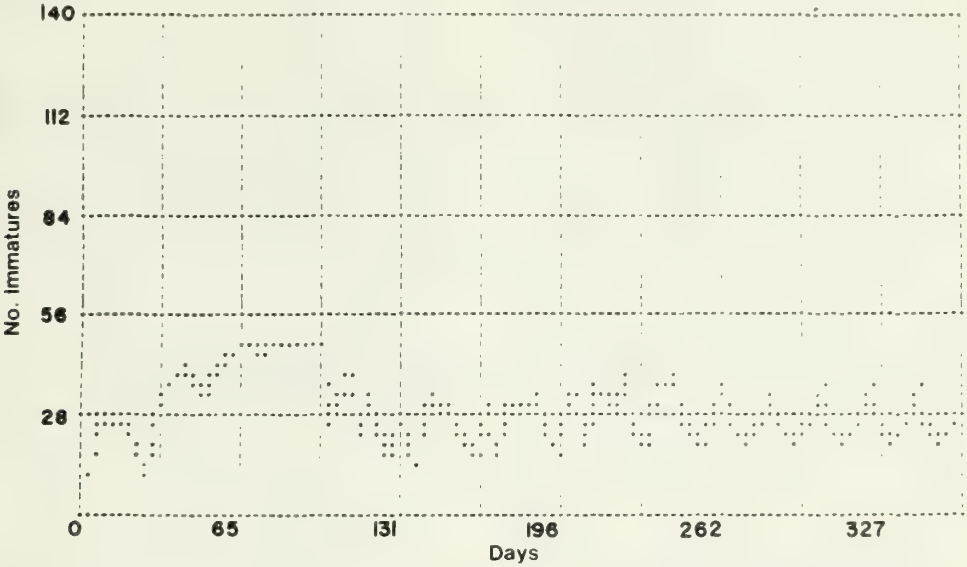

FIGURE 11.—*Aedes aegypti* immature density following contact adulticide application when *Aedes aegypti* adult density exceeded seven adults per container (no rain).

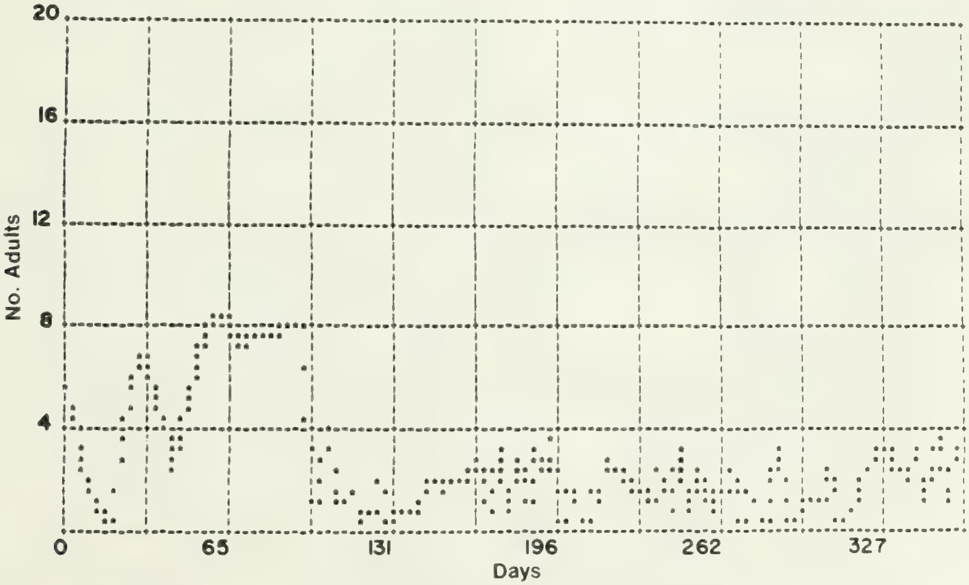

FIGURE 12.—*Aedes aegypti* adult density following contact adulticide application when *Aedes aegypti* adult density exceeded four adults per container (no rain). Spraying at this density required 21 applications in 262 days.

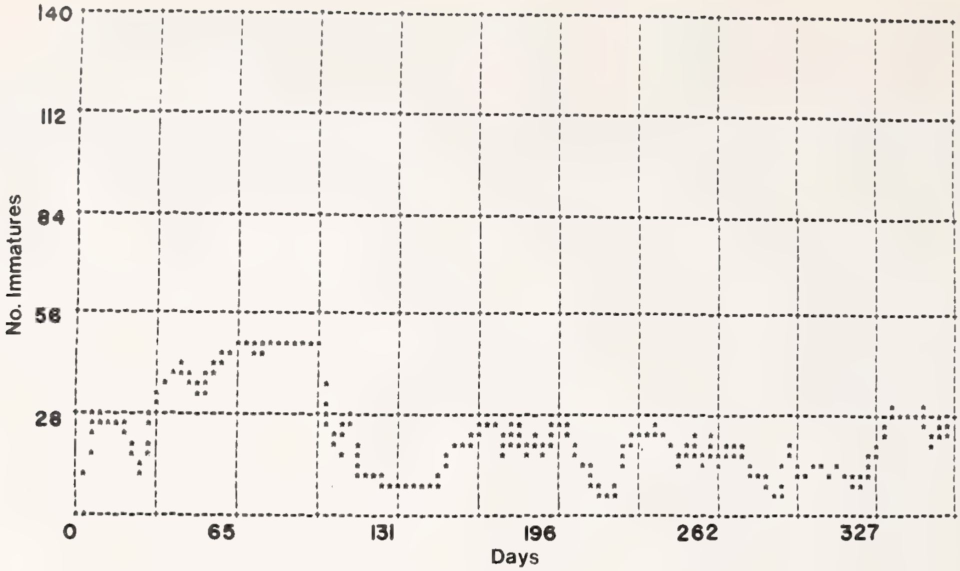

FIGURE 13.—*Aedes aegypti* immature density following contact adulticide application when *Aedes aegypti* adult density exceeded four adults per container (no rain).

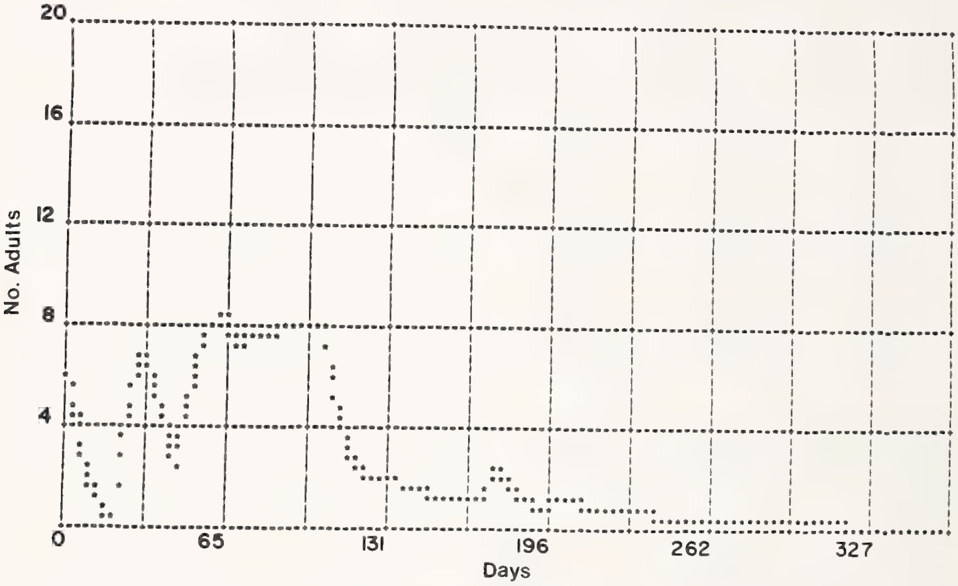

FIGURE 14.—*Aedes aegypti* adult density following an adult predator release on day 98 that resulted in one predator egg in 80% of the containers positive for prey (no rain).

application. Figures 10 and 12 show the increased frequency of application required to maintain an increasingly lower adult density. Because of this type of situation, population suppression has usually involved the use of larvicides in addition to adulticides (Gould, et al. 1970, 1971).

Figure 14 shows the effects of a predator release on day 98 that resulted in one predator egg in 80% of the containers during a period of no rainfall. A 75% reduction in *Ae. aegypti* adult density occurred within 20 days. The *Ae. aegypti* adult blip beginning about day 170 resulted from the eclosion of the predator. The effects of the subsequent second generation of predators resulting from the release are shown after day 185 in figure 14.

Until actual field trials are made, the reality of the effects of a second generation will remain uncertain. The model does depict, however, smaller and smaller subsequent generations of predator. These results are consistent with known equilibrium densities of predator and prey in nature.

Figure 15 reveals that one predatory larva was sufficient to deplete a water-storage container in 6 to 8 days. The model further shows that continued oviposition by declining numbers of *Ae. aegypti* provided food, allowing the predator to develop and eclose in approximately 53 days.

Simulations involving larger adult releases that produced greater numbers of predator eggs per container did not appreciably alter the *Ae. aegypti* decline. This is understandable because one predator per container was sufficient to stop prey breeding in that particular container; therefore, the additional predators were superfluous. Larger numbers of predators per container further exacerbated the prey shortage, producing even longer development times. In the field, a variable number of predators per container would likely result in asynchronous predator eclosion.

Since rainfall increased the number of young prey larvae, five predators per container were required to eliminate *Ae. aegypti* breeding in containers positive for *Tx. r. rutilus*. Figure 16 shows the failure of three predators per container to establish control. Furthermore, the increased food supply caused shorter predator development times, which resulted in shorter periods of control from the first cohort of predators. The ramifications of this would depend on the results of subsequent generations of predators resulting from the original release. At any rate, the lower numbers of predators required in the dry season to initiate control indicate a logical time to attempt control.

Figures 17, 18, and 19 represent expected *Ae. aegypti* adult densities when the percentage of

(*Continued on page 16.*)

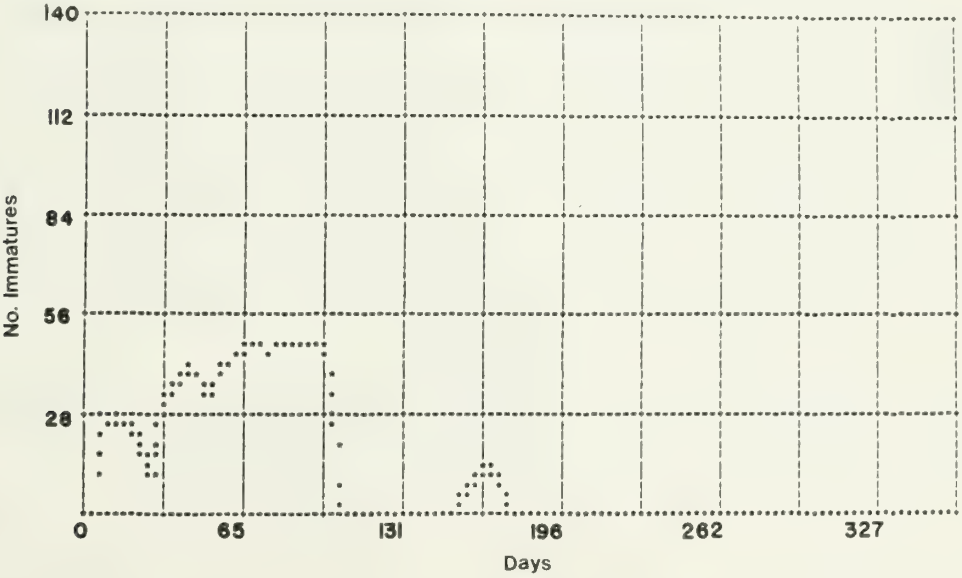

FIGURE 15.—*Aedes aegypti* immature density following release of one predatory larva per container on day 98 in 80% of the containers positive for *Aedes aegypti* (no rain). The blip at 160 days is a result of predator eclosion from the container.

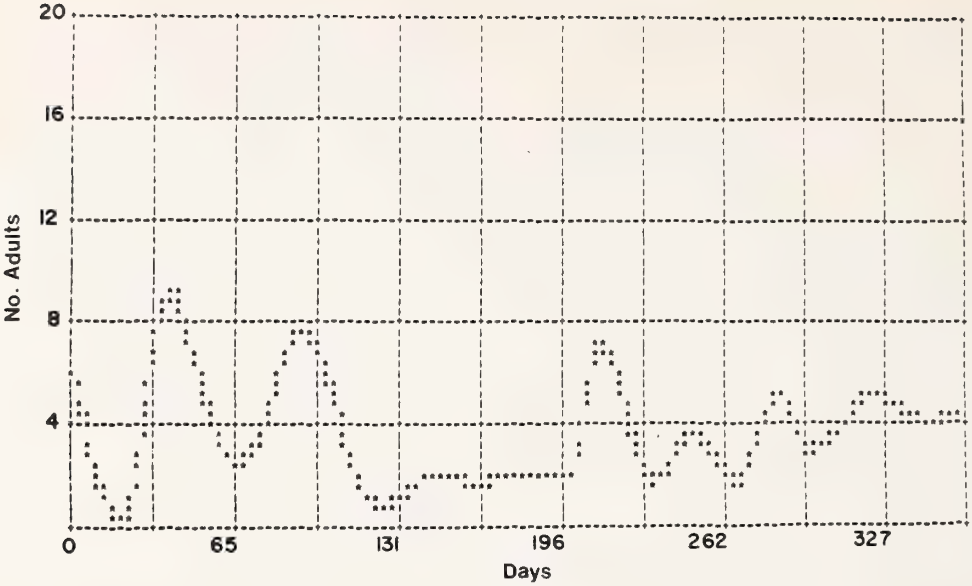

FIGURE 16.—*Aedes aegypti* adult density following an adult predator release on day 98 that resulted in three predatory larvae per container in 80% of the containers positive for *Aedes aegypti* (daily rain).

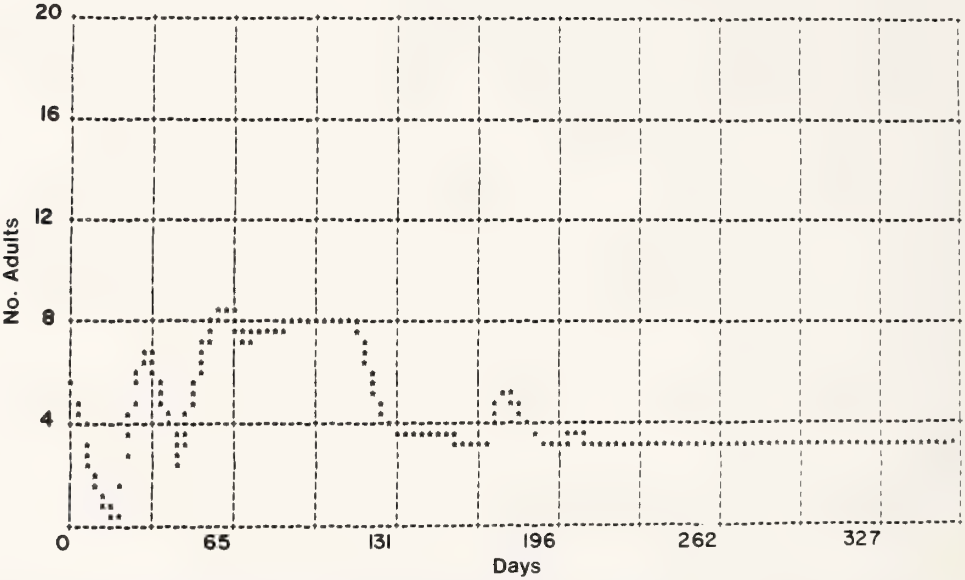

FIGURE 17.—*Aedes aegypti* adult density following an adult predator release on day 107 that resulted in one predator egg per container in 60% of the containers positive for *Aedes aegypti* immatures (no rain).

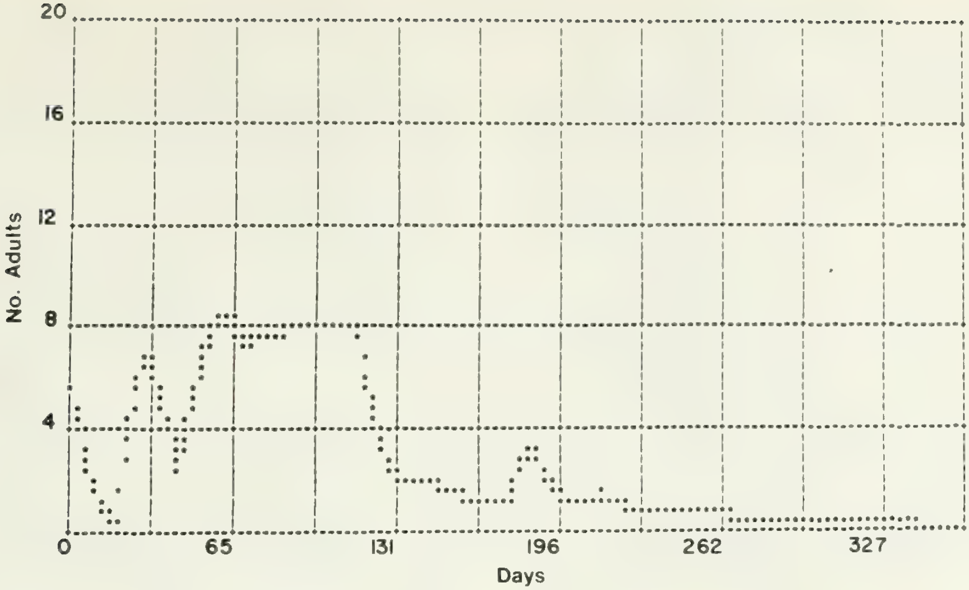

FIGURE 18.—*Aedes aegypti* adult density following an adult predator release on day 107 that resulted in one predator egg per container in 80% of the containers positive for *Aedes aegypti* immatures (no rain).

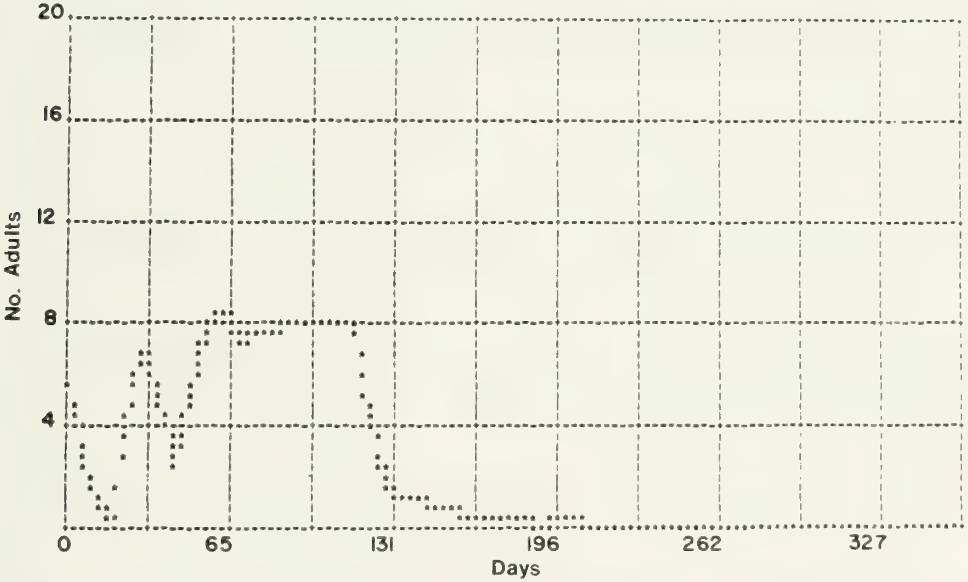

FIGURE 19.—*Aedes aegypti* adult density following an adult predator release on day 107 that resulted in one predator egg per container in 90% of the containers positive for *Aedes aegypti* (no rain).

containers receiving one predator egg per container is 60%, 80%, and 90%, respectively. The preceding discussion and these figures lend support to the idea that the most important parameter determining the degree of control established is the distribution of predator eggs (=DISTBN). It seems likely that energy would be well spent in improving predator distribution through release of smaller numbers of adults at more sites.

Simulations involving the use of adulticides

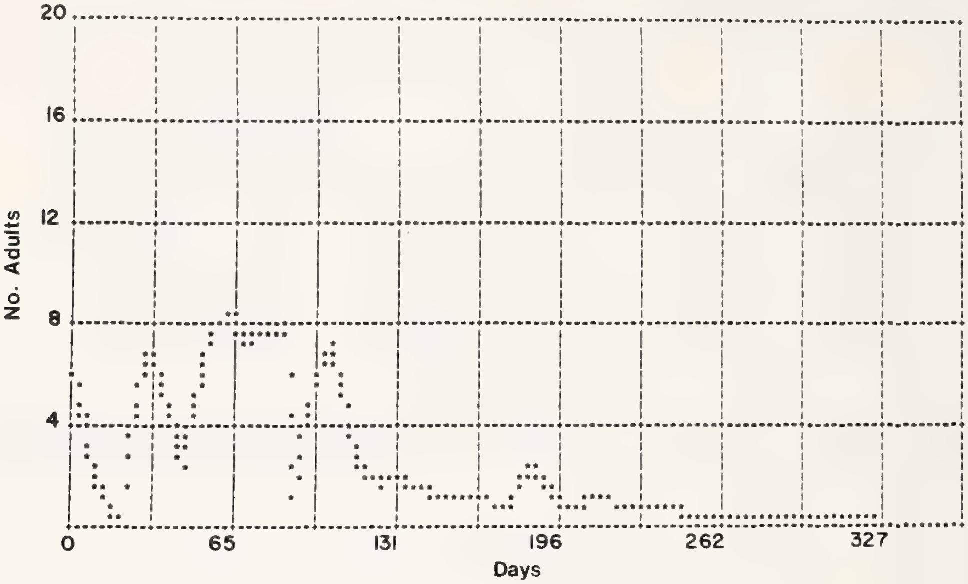

FIGURE 20.—*Aedes aegypti* adult density following contact adulticide application on day 90 and subsequent predator release on day 98 (no rain). Compare results with those in figures 8 and 14.

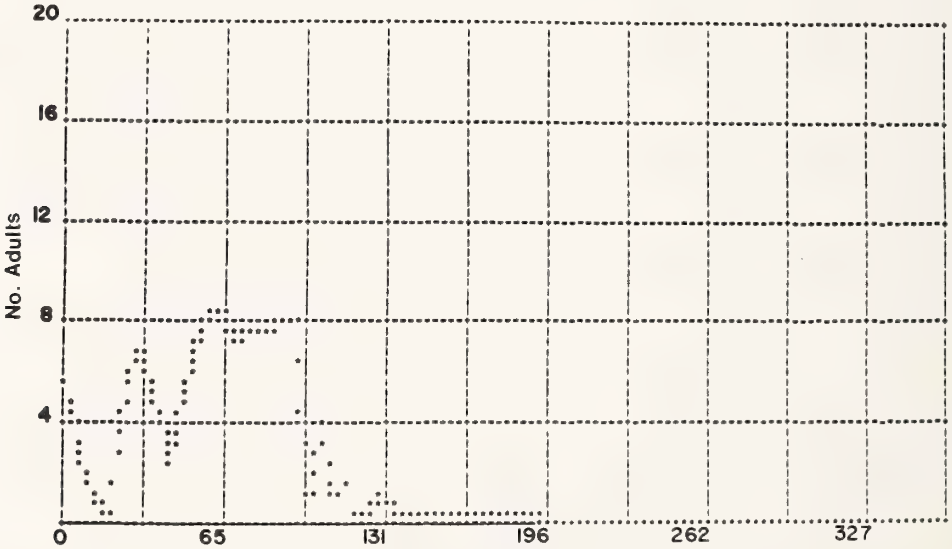

FIGURE 21.—*Aedes aegypti* adult density following a predator release and five subsequent contact adulticide applications on days 98, 101, 109, 113, and 117 when *Aedes aegypti* adult density exceeded four adults per container (no rain). Compare results with those in figures 12 and 14.

and predators revealed the following: (1) One adulticide application shortly before or after a predator release did not significantly decrease the resulting prey density nor increase the rate at which it was achieved (fig. 20). (2) Several applications 2 or 3 days apart after a predator release resulted in immediate and sustained prey densities near zero (fig. 21). These results reenforce our assumption that maintenance of control is a function of the efficacy of the resulting subsequent predator generations.

CONCLUSIONS

As stated previously, the computer model is a useful tool in evaluating and developing new control strategies. The utility of *Tx. r. rutilus* in controlling container-breeding mosquitoes will have to be demonstrated in the field rather than in a computer. Demonstrated here is the feasibility of control and a justification for larger scale fieldwork than has already been done.

Field data on predator distribution, the effects of second- and third-generation predators resulting from an initial release, and field-survival values for the immature predator stages will make it possible to develop an accurate stochastic model. This model, in turn, will facilitate the evaluation of a strategy involving insecticides, predators, and the sterile-male technique.

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APPENDIX.—FORTRAN LISTING

```
      REAL GRAPH(3000), DAY(360), SUMA(360), SUMTA(360),
     1SUM1(360), SUM2(360), SUM3(360), X1(360), X2(360),
     1X3(360), X4(360), X5(360), X6(360), X7(360)
      DATA DAY, SUMA, SUMTA, SUM1, SUM2, SUM3, X1, X2,
     1X3, X4, X5, X6, X7/ 360*0., 360*0., 360*0., 360*0.,
     1360*0., 360*0., 360*0., 360*0., 360*0., 360*0., 360*0., 360*0.,
     1360*0.    /
      REAL B1(360), B2(360), B3(360), B4(360)
      DATA B1,B2,B3,B4/360*0.,360*0.,360*0.,360*0./
      REAL C1(360),C2(360),C3(360),C4(360)
      DATA C1,C2,C3,C4/ 360*0.,360*0.,360*0.,360*0./
      REAL D1(360)
      DATA D1/360*0./
      REAL B5(360), C5(360)
      DATA B5,  C5  /360*0.,360*0./
      REAL A(8),TA(7)
C            A & TA REPRESENT AEDES & TOX. ADULTS
C
      REAL E(6),X(5),Y(12)
C            AEDES IMMATURES IN CONTAINERS WITHOUT TOX.
C            WHERE E=EGGS, X=STAGES 1&2,& Y=STAGES 3,4&PUPA.
C
      REAL TEMP12(24), TEMP3(40), TEMP4(108)
      DATA  TEMP12, TEMP3, TEMP4 /24*0., 40*0., 108*0.  /
      REAL ET(6),XA(5),YA(12)
C            AEDES IMMATURES IN CONTAINERS POSITIVE FOR TOX.
C            ET=AE.EGGS, XA=AE.STAGES 1&2 & YA REPRESENTS STAGES 3-PUPA
C
      REAL  T12(24),T3(40),T4(108),TP(8), TE(3)
C            TOXORHYNCHITES IMMATURE ARAYS; T12=STAGES 1&2, T3=STAGE 3
C            T4=STAGE-4, TP=PUPA, &TE=EGGS
C
      DATA  A,TA/ 8*0.,7*0.   /
      DATA  E,X,Y/ 6*0.,5*0.,12*0. /
      DATA  ET,XA,YA/ 6*0.,5*0.,12*0.  /
      DATA  T12,T3,T4,TP/ 24*0.,40*0.,108*0.,8*0. /
      DATA  TE/ 3*0.   /
      I=0
C
C            AEDIST=PROPORTION OF CONTAINERS POSITIVE FOR AEDES LARVAE
      SA=0.88
C            SA=ADULT DAILY SURVIVAL
      F=93
C            F=FECUNDITY (EGGS/BATCH)
      P=0.90
C            P=PROPORTION OF PUPATION WHICH IS SUCCESSFUL
      SE=0.98
C            SE=DAILY EGG SURVIVAL
      S=0.95
C            S=DAILY SURVIVAL FOR STAGES 3,4 & PUPA
      C=0.01
C            C=DENSITY DEPENDENT COEFFICIENT FOR CALCULATING
C            SI,WHERE SI=DAILY LARVAL SURVIVAL,STAGES 1 &2.
C
C
C        ***TOX. PARAMETERS***
      SAT=0.88
C            SAT=DAILY ADULT SURVIVAL.
      FT=1.0
C            FT=DAILY EGG PRODUCTION.
      SIT=0.99
C            SIT=DAILY IMMATURE SURVIVAL, STAGES 1-PUPA.
C            DISTBN=PROPORTION OF CONTAINERS POSITIVE FOR TOX. EGGS.
      DISTBN=0.80
C     ************************************************************
      IRAIN=1
 1000 I=I+1
C            INITIALIZE AEDES WITH 7.4 ADULTS/CONTAINER
      IF(I.EQ.1) A(1)=7.4
C     BELOW REPRESENTS AN ADULTICIDE APPLICATION CAUSING 95% MORTALITY
      IF(I.LT.98) GOTO 1501
C     R=ADULT DENSITY WHEN ULV IS APPLIED
```

```
      R=1000
      SA=0.88
      IF (SUMA(I-1).GT.R) SA=0.05
      IF(SA.EQ..05) GOTO 1500
      GOTO 1501
 1500 WRITE (6,1502) I
 1502 FORMAT (1X,I3)
 1501 CONTINUE
      IF (I.EQ.107) TE(1)=1
C             ***AEDES ADULTS***
      A(8)=A(7)*SA
      A(7)=A(6)*SA
      A(6)=A(5)*SA
      A(5)=A(4)*SA
      A(4)=A(3)*SA+A(8)*SA
      A(3)=A(2)*SA
      A(2)=A(1)*SA
      A(1)=(Y(12)*P*(1-DISTBN))+(YA(12)*P*DISTBN)
C             ***AEDES LARVAE IN CONTAINERS WITHOUT TOX. LARVAE***
C
C     FOLLOWING MOVES STAGES 3-PUPA
  150 Y(12)=Y(11)*S
      Y(11)=Y(10)*S
      Y(10)=Y(9)*S
      Y(9)=Y(8)*S
      Y(8)=Y(7)*S
      Y(7)=Y(6)*S
      Y(6)=Y(5)*S
      Y(5)=Y(4)*S
      Y(4)=Y(3)*S
      Y(3)=Y(2)*S
      Y(2)=Y(1)*S
C     FOLLOWING CALCULATES SI FOR STAGES 1 AND 2
      SUM=X(1)+X(2)+X(3)+X(4)+X(5)
      IF(SUM.EQ.0) SI=1.0
      IF(SUM.EQ.0) GOTO 30
      IF(SUM.LT.15) GOTO 10
      IF(SUM.GT.120) GOTO 20
      XNT= SUM*(EXP(-C*SUM))
      SI=XNT/SUM
      GOTO 30
   10 SI=0.88
      GOTO 30
   20 SI=120/SUM
C     FOLLOWING MOVES STAGES 1 AND 2
   30 Y(1)=X(5)*SI
      X(5)=X(4)*SI
      X(4)=X(3)*SI
      X(3)=X(2)*SI
      X(2)=X(1)*SI
C               THE FOLLOWING CONTROLS EGG HATCH& OVIPOSITION
      E(6)=(E(5)+E(6))*SE
      E(5)=E(4)*SE
      E(4)=E(3)*SE
      E(3)=E(2)*SE
      E(2)=E(1)*SE
C
C               AEDES OVIPOSITION INTO TOX-FREE CONTAINERS
      E(1)=A(4)*F*0.5
C               EGG HATCH AS FUNCTION OF RAINFALL (IRAIN)
      IF(IRAIN.EQ.1) GOTO 100
      X(1)=E(5)*0.2
      E(5)=E(5)*0.8
      GOTO 200
  100 X(1)=E(6)*0.5+(E(5)*0.2)
      E(6)=E(6)*0.5
      E(5)=E(5)*0.8
  200 CONTINUE
C             ***AEDES LARVAE IN CONTAINERS WITH TOX. LARVAE***
C
C     FOLLOWING MOVES STAGES 3-PUPA
  151 YA(12)=YA(11)*S
      YA(11)=YA(10)*S
      YA(10)=YA(9)*S
      YA(9)=YA(8)*S
      YA(8)=YA(7)*S
```

```
     YA(7)=YA(6)*S
     YA(6)=YA(5)*S
     YA(5)=YA(4)*S
     YA(4)=YA(3)*S
     YA(3)=YA(2)*S
     YA(2)=YA(1)*S
     FOLLOWING CALCULATES SIX FOR STAGES 1 AND 2
     SCMA=XA(1)+XA(2)+XA(3)+XA(4)+XA(5)
     IF(SOMA.EQ.0) SIX=1.0
     IF(SOMA.EQ.0) GOTO 31
     IF(SOMA.LT.15) GOTO 11
     IF(SOMA.GT.120) GOTO 21
     XNTA= SOMA*(EXP(-C*SOMA))
     SIX=XNTA/SOMA
     GOTO 31
  11 SIX=0.88
     GCTO 31
  21 SIX=120/SOMA
     FOLLOWING MOVES STAGES 1 AND 2
  31 YA(1)=XA(5)*SIX
     XA(5)=XA(4)*SIX
     XA(4)=XA(3)*SIX
     XA(3)=XA(2)*SIX
     XA(2)=XA(1)*SIX
              THE FOLLOWING CONTROLS EGG HATCH& OVIPOSITION
     ET(6)=(ET(5)+ET(6))*SE
     ET(5)=ET(4)*SE
     ET(4)=ET(3)*SE
     ET(3)=ET(2)*SE
     ET(2)=ET(1)*SE

              AEDES OVIPOSITION INTO CONTAINERS POSITIVE FOR TUX.
     ET(1)=A(4)*F*0.5
              EGG HATCH AS FUNCTION OF RAINFALL (IRAIN)
     IF(IRAIN.EQ.1) GOTO 101
     XA(1)=ET(5)*0.2
     ET(5)=ET(5)*0.8
     GCTC 201
 101 XA(1)=ET(6)*0.5+(ET(5)*0.2)
     ET(6)=ET(6)*0.5
     ET(5)=ET(5)*0.8
 201 CONTINLF
            ***BELOW REPRESENTS TOX. IMMATURES & THEIR PREDATIUN***
                    ON AEDES LARVAE IN THE ABOVE SECTION

              THE FOLLWCING INTERFACES 1&2-STAGE AEDES
              WITH 1&2-STAGE TOX.
     SMXA1=0
     SMXA1=NO. 1&2-STAGE AE. LARVAE IN AE./TX. CONTAINER
     DO 13 KN=1,5
  13 SMXA1=XA(KN)+SMXA1
     SMT12=0
     SMT12=NO. 1&2-STAGE TOX. LARVAE
     DC 71 M=1,16
  71 SMT12=SMT12+T12(M)
     IF(SMXA1.GT.SMT12*4) GCTO 29
     IF(SMXA1.EQ.0) IZ=1
     IF(SMXA1.EQ.0) GOTO 39
     IF(SMT12.EQ.0) GOTO 601
     IZ= INT(SMXA1/SMT12)
     IF(IZ.EQ.0) IZ=1
     DC 61 L=1,5
  61 XA(L)=0
     GOTO 39
  29 IZ=4
     ATE=(4*SMT12)
     IF(ATE.EQ.0) GOTO 39
     BB=ATE/SMXA1
     CC=1-BB
     DC 52 K=1,5
  52 XA(K)=XA(K)*CC
  39 CONTINLE
     DC 41 J=1,16
     TEMP12(J+IZ)=T12(J)*SIT
  41 CONTINUE
     DC 999 MM=1,24
  999 T12(MM)=TEMP12(MM)
  601 CONTINUE
C
C                THE FOLLOWING INTERFACES 3&4-STAGE TOX. WITH ALL STAGES
C                OF AEDES IMMATURES. MODEL ASSUMES AEDES 1&2-STAGE LARVAE
C                ARE EATEN FIRST FOLLOWED BY 3,4&P-STAGE AEDES. NOTICE
C                THAT FOR EACH DAY,THE 1&2-STAGE TOX. EAT FIRST.
      T3(1)=T12(17)+T12(18)+T12(19)+T12(20)
      DO 400 K30=17,20
      T12(K30)=0
  400 CONTINUE
C                SMXA2=NO. AEDES LARVAE,STAGE 1&2,AVAILABLE AS FOUD.
      SMXA2=0
      DC 53 N=1,5
   53 SMXA2=SMXA2+XA(N)
C                SMY=NO. 3,4& PUPAL-STAGE AEDES AVAILABLE AS FOOD.
      SMY=0
      DO 32 LL=1,12
   32 SMY=SMY+YA(LL)
      TOTU=SMXA2+(SMY*7.1111)
C                NOTE-1 3,4 OR PUPA-STAGE AEDES IS EQUIVLENT TO 7.111
C                1 OR 2-STAGE AEDES LARVAE. TOTU=AMOUNT OF FOOD AVAILABLE.
C                ST3=NO. 3-STAGE TOX., ST4=NO. 4-STAGE TOX.
      ST3=0
      DC 42 II=1,32
   42 ST3=ST3+T3(II)
      ST4=0
      DO 85 JJ=1,96
      ST4=ST4+T4(JJ)
   85 CONTINUE
C                REQ3&4 ARE THE NO. OF AEDES EQUIV. NECESSARY TO MOVE 1
C                REGULAR DAY.
      REQ3=ST3*14
      REQ4=ST4*64
      TREQ=REQ3+REQ4
      IF(TOTU.EQ.0) IT3=1
      IF(TOTU.EQ.0) IT4=1
      IF(TOTU.EQ.0) GOTO 105
      IF(TREQ.EQ.0) GOTO 108
      IF(TREQ.LE.TOTU) GOTO 115
      DC 22 KK=1,5
      XA(KK)=0
   22 CONTINUE
      DO 12 KI=1,12
      YA(KI)=0
   12 CONTINUE
      Q=TOTU/TREQ
C     IT3&4 INCREMENT THEIR RESPECTIVE ARAYS WHEN LESS THAN MIN. FOOD
C               IS AVAILABLE.
      IT3=INT(8*Q)
      IT4=INT(12*Q)
      IF (IT3.EQ.0) IT3=1
      IF (IT4.EQ.0) IT4=1
      GCTC 105
  115 IT3=8
      IT4=12
C     ITERATIONS FOR 3&4-STAGE TOX. WHEN AMPLE FOOD AVAILABLE.
      BAL=TREG-SMXA2
C     BAL HERE REPRESENTS THE NO. UNITS REQD. FROM YA.
      IF(BAL.GT.0) GOTO 90
      SIAX=ABS(BAL/SMXA2)
      DO 91 MI=1,5
   91 XA(MI)=XA(MI)*SIAX
      GCTO 105
   90 CONTINUE
      DO 92 MJ=1,5
   92 XA(MJ)=0
      BAL=ABS(BAL)
      SIYA=((SMY*7.111)-BAL)/(SMY*7.111)
      DO 125 IN=1,12
  125 YA(IN)=YA(IN)*SIYA
  105 CONTINUE
      DO 106 KJ=1,32
      TEMP3(KJ+IT3)=T3(KJ)*SIT
  106 CCNTINUE
      DO 998 M5=1,40
```

```
    T3(M5)=TEMP3(M5)
998 CONTINUE
    DO 107 KM=1,96
    TEMP4(KM+IT4)=T4(KM)*SIT
107 CONTINUE
    DO 997 M6=1,108
    T4(M6)=TEMP4(M6)
997 CONTINUE
    T4(1)=0
    DO 555 LM=33,40
    T4(1)=T4(1)+T3(LM)
555 CONTINUE
    DO 401 K31=33,40
    T3(K31)=0
401 CONTINUE
108 CONTINUE
    TP(7)=TP(6)*SIT
    TP(6)=TP(5)*SIT
    TP(5)=TP(4)*SIT
    TP(4)=TP(3)*SIT
    TP(3)=TP(2)*SIT
    TP(2)=TP(1)*SIT
    TP(1)=0
    DO 996 M7=97,108
    TP(1)=TP(1)+T4(M7)
996 CONTINUE
    DO 402 I31=97,108
    T4(I31)=0
402 CONTINUE
    TA(7)=(TA(7)+TA(6))*SAT
    TA(6)=TA(5)*SAT
    TA(5)=TA(4)*SAT
    TA(4)=TA(3)*SAT
    TA(3)=TA(2)*SAT
    TA(2)=TA(1)*SAT
    TA(1)=TP(7)*SIT
    TE(3)=TE(2)
    TE(2)=TE(1)
    TOX. OVIPOSITION & EGGS
    TE(1)=TA(7)*0.5*FT*AEDIST
    T12(1)=TE(3)
    C1(I)=Y(1)+Y(2)+Y(3)+Y(4)
    C2(I)=Y(5)+Y(6)+Y(7)+Y(8)+Y(9)+Y(10)
    C3(I)=Y(11)+Y(12)
    C1,2 &3 ARE THE NO. OF AE. STAGE 3,4 AND PUPA
        IN CONTAINERS WITHOUT TX.
    C4(I)=SI
    C5(I)=SIX
    SUMA & SUMTA ARE THE NO. OF AE. AND TOX. ADULTS.
    SUMA(I)=0
     DO 801 J1=1,8
    SUMA(I)=SUMA(I)+A(J1)
801 CONTINUE
    SUMTA(I)=0
    DO 802 J2=1,7
802 SUMTA(I)=SUMTA(I)+ TA(J2)
    DAY(I)=I
    D1(I)=0
    DO 803 J3=1,5
803 D1(I)=D1(I)+X(J3)
    X2(I)=0
    DO 804 J4=1,12
804 X2(I)=X2(I)+Y(J4)
    SUM1(I)=D1(I)+X2(I)
    SUM1=SUM OF AE. IMMATURES IN CONTAINERS WITHOUT TX. LARVAL.
    X3(I)=0
    DO 805 J6=1,5
805 X3(I)=X3(I)+XA(J6)
    X4(I)=0
    DO 806 J7=1,12
806 X4(I)=X4(I)+YA(J7)
    SUM2(I)=X3(I)+X4(I)
    SUM2=SUM OF AE. IMMATURES IN CONTAINERS POSITIVE FOR TX. LARVAE.
    X5(I)=0
    DO 807 J7=1,16
807 X5(I)=X5(I)+T12(J7)
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      X6(I)=0
      DO 808 J8=1,32
  808 X6(I)=X6(I)+T3(J8)
      X7(I)=0
      DO 809 J9=1,96
  809 X7(I)=X7(I)+T4(J9)
      SUM3(I)=X5(I)+X6(I)+X7(I)
C     SUM3=SUM OF TX. LARVAE.
      IF(I.LT.360) GOTO 1000
      DO 308 I=1,357
  308 X1(I)=(D1(I)+D1(I+1)+D1(I+2)+D1(I+3))/4
      DO 304 I=1,357
  304 B1(I)=(C1(I)+C1(I+1)+C1(I+2)+C1(I+3))/4
      DO 305 I=1,357
  305 B2(I)=(C2(I)+C2(I+1)+C2(I+2)+C2(I+3))/4
      DO 306 I=1,357
  306 B3(I)=(C3(I)+C3(I+1)+C3(I+2)+C3(I+3))/4
      DO 307 I=1,357
  307 B4(I)=(C4(I)+C4(I+1)+C4(I+2)+C4(I+3))/4
      DO 501 I=1,357
  501 SUMA(I)=(SUMA(I+1)+SUMA(I)+SUMA(I+2)+SUMA(I+3))/4
      DO 502 I=1,357
  502 SUMTA(I)=(SUMTA(I)+SUMTA(I+1)+SUMTA(I+2)+SUMTA(I+3))/4
      DO 503 I=1,357
  503 SUM1(I)=(SUM1(I)+SUM1(I+1)+SUM1(I+2)+SUM1(I+3))/4
      DO 504 I=1,357
  504 SUM2(I)=(SUM2(I)+SUM2(I+1)+SUM2(I+2)+SUM2(I+3))/4
      DO 505 I=1,357
  505 SUM3(I)=(SUM3(I)+SUM3(I+1)+SUM3(I+2)+SUM3(I+3))/4
      DO 471 I=1,357
  471 B5(I)=(C5(I)+C5(I+1)+C5(I+2)+C5(I+3))/4
C     BELOW PLOTS AE. ADULTS
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH,360.,0.,20.,0.)
      CALL PLOT3 (1H*,DAY(1),SUMA(1),357)
      WRITE (6,700)
  700 FORMAT (1H1, 'AEDES ADULTS')
      CALL PLOT4 (12,12HAEDES ADULTS)
      WRITE (6,1200)
C     BELOW PLOTS TX. ADULTS
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH,360.,0.,20.,0.)
      CALL PLOT3(1H*,DAY(1),SUMTA(1),357)
      WRITE(6,701)
  701 FORMAT(1H1,'TOXORHYNCHITES ADULTS')
      CALL PLOT4(11,11HTOX. ADULTS)
      WRITE (6,1200)
C     BELOW PLOTS AE. IMMATURES IN CONTAINERS WITHOUT TX.
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2(GRAPH,360.,0.,140.,0.)
      CALL PLOT3(1H*,DAY(1),SUM1(1),357)
      WRITE (6,702)
  702 FORMAT (1H1,'AE. IMMATURES IN CONTAINERS WITHOUT TX. IMMATURES')
      CALL PLOT4(15,15 HAEDES IMMATURES)
      WRITE(6,1200)
C     BELOW PLOTS AE. STAGE 1 & 2
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH,360.,0.,140.,0.)
      CALL PLOT3 (1H*,DAY(1),X1(1),357)
      WRITE (6,705)
  705 FORMAT (1H1,'AE. STAGES-1&2 IN CONTAINERS WITHOUT TX. LARVAE')
      CALL PLOT4 (9,9HAEDES 1&2)
      WRITE (6,1200)
C     BELOW PLOTS AE. STAGE 3
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH,360.,0.,50.,0.)
      CALL PLOT3 (1H*,DAY(1),B1(1),357)
      WRITE (6,300)
  300 FORMAT (1H1,'AE. STAGE-3 IN CONTAINERS WITHOUT TX. LARVAE')
      CALL PLOT4 (13,13HAEDES STAGE 3)
      WRITE (6,1200)
C     BELOW PLOTS AE. STAGE- 4
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH,360.,0.,25.,0.)
      CALL PLOT3 (1H*,DAY(1),B2(1),357)
      WRITE (6,301)
  301 FORMAT (1H1,'AE. STAGE-4 IN CONTAINERS WITHOUT TX. LARVAE')
      CALL PLOT4 (13,13HAEDES STAGE 4)
      WRITE (6,1200)
C     BELOW PLOTS AE. PUPAE
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH,360.,0.,10.,0.)
      CALL PLOT3 (1H*,DAY(1),B3( 1),357)
      WRITE (6,302)
  302 FORMAT (1H1,'AE. PUPAE IN CONTAINERS WITHOUT TX. LARVAE')
      CALL PLOT4 (11,11HAEDES PUPAE)
      WRITE (6,1200)
C     BELOW PLOTS SI
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH, 360.,0.,1.,0.)
      CALL PLOT3 (1H*,DAY(1),B4(1),357)
      WRITE (6,303)
  303 FORMAT (1H1,'IMMATURE SURVIVAL (SI) FOR STAGES 1&2 AEDES IN
     XCONTAINERS WITHOUT TX.')
      CALL PLOT4 (2,2HSI)
      WRITE (6,1200)
C     BELOW PLOTS SIX
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH,360.,0.,1.,0.)
      CALL PLOT3 (1H*, DAY(1), B5(1),357)
      WRITE (6,450)
  450 FORMAT (1H1,'IMMATURE SURVIVAL (SIX) FOR AEDES STAGES-1&2 IN
     1CONTAINERS POSITIVE FOR TX.')
      CALL PLOT4 (2,2HSI)
      WRITE (6,1200)
C     BELOW PLOTS AE. IMMATURES IN CONTAINERS WITH TX.
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2(GRAPH,360.,0.,140.,0.)
      CALL PLOT3 (1H*,DAY(1),SUM2(1),357)
      WRITE (6,703)
  703 FORMAT (1H1,'AE. IMMATURES IN CONTAINERS POSITIVE FOR TX. LARVAE')
      CALL PLOT4 (15,15HAEDES IMMATURES)
      WRITE (6,1200)
C     BELOW PLOTS TX. LARVAE
      CALL PLOT1 (3,51,10,111,10)
      CALL PLOT2 (GRAPH,360.,0.,20.,0.)
      CALL PLOT3(1H*,DAY(1),SUM3(1),357)
      WRITE (6,704)
  704 FORMAT (1H1,'TOXORHYNCHITES LARVAE')
      CALL PLOT4 (11,11HTOX  LARVAE)
      WRITE (6,1200)
 1200 FORMAT (1H0,53X,'DAY')
      STOP
      END
$ENTRY
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